What omnivores don't eat

Nonconsumptive ecological effects of phytophagy by Macrolophus pygmaeus

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Plant feeding by an omnivorous predator affects plant phenology and omnivore performance

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ABSTRACT – Plant feeding by omnivorous predators can induce plant defences that decrease the performance of herbivores and influence behaviour of other predators. However, it is not known what are the consequences of this feeding for the plant and how this, in turn, affects the omnivore. We therefore investigated the effects of the omnivorous predator *Macrolophus pygmaeus* on plant development and reproduction. We found that sweet pepper plants exposed to *M. pygmaeus* had significantly fewer leaves and open flowers than clean plants, but numbers of fruits were similar in both treatments. Moreover, the presence of the omnivore significantly shortened the period for flowers to become fruits. The dry weights of leaves plus stems and fruits were similar on clean plants and plants with the omnivore. Significantly higher numbers of seeds were found in fruits from plants exposed to the omnivore than those of clean plants. The survival rates of *M. pygmaeus* females and nymphs were positively related with numbers of flowers on the plants. Our results show that the presence of this omnivorous predator can benefit plants by increasing seed production; however, the changes in plant phenology do not seem to benefit the omnivore.

Introduction

Plants face many biotic and abiotic challenges, of which herbivory is one of the most severe. Herbivory on flowers and other reproductive tissues can directly affect plant reproduction by decreasing the number of flowers, fruits and seeds (Bertness et al. 1987; Cunningham 1995; Krupnick and Weis 1999; McCall and Irwin 2006). Removal of leaf tissue by herbivores can cause reduction in photosynthesis, suppression of plant growth and reduced biomass (Marquis 1984; Poveda et al. 2003; Lemoine et al. 2017). Leaf damage can also alter flower phenology and morphology, affecting plant reproduction. Herbivory on leaves can delay flowering time (Hanley and Fegan 2007), decrease the number of flowers (Karban and Strauss 1993; Frazee and Marquis 1994) and the size of flowers (Strauss 1997). For example, foliar herbivory by cabbage white butterfly larvae delayed flowering time and decreases flower size of wild radish plants, but did not affect the plant size and biomass, or the lifetime flower production and total number of fruits and seeds (Strauss et al. 1996; Lehtilä and Strauss 1997, 1999). Herbivory on leaves and flowers may also change pollen and nectar characteristics. For instance, foliar herbivory on wild radish plants by cabbage white butterfly larvae reduced the amount and size of pollen (Lehtilä and Strauss 1999). A perennial shrub exposed to a pollen beetle produced fewer functional inflorescences than unexposed plants, and flowers damaged by beetles produced less than one third of the amount of nectar per flower than undamaged flowers (Krupnick and Weis 1999), and tobacco hornworm herbivory on tobacco leaves increased alkaloids in nectar, but not in leaves (Adler et al. 2006).

Furthermore, herbivory on leaves and flowers can change the emission of plant volatiles (Kessler and Halitschke 2009). Bruinsma et al. (2014) showed that the emission of volatiles from flowers changed significantly upon attacks of black mustard leaves by caterpillars. Another study found that flower herbivory reduced volatile emission from black mustard plants (Lucas-Barbosa et al. 2013).

Phenological, morphological and physiological changes caused by herbivory can also affect other organisms on the plant, such as other species of herbivores, predators and flower visitors, including pollinators, which may alter plant reproduction (Ohgushi et al. 2007). Delayed flowering time may cause plants missing the peak of pollinator activity, resulting in a lower flower visiting rate (Sharaf and Price 2004). Changes in flower size and number, and in pollen and nectar characteristics alter the attraction of flower visitors, which affects plant reproduction (Mothershead and Marquis 2000; Hoffmeister et al. 2016). A study by Strauss et al. (1996) shows that foliar herbivory delayed flowering time, decreased flower size and pollen production, resulting in reduction in the number and duration of visits of pollinators. Such reduction of pollinator visits can affect plant reproduction because it can result in reduced seed set (Adler et al. 2001).

Plants are not passive victims when facing herbivore attacks,; they employ different strategies to reduce the negative effects of herbivory. In response to herbivore attacks, plants defend themselves through constitutive as well as induced defences (Karban and Baldwin 1997; Kant et al. 2015). These defences can lower the performance of herbivores directly by the induction of production of specific secondary compounds upon herbivore attack, referred to as induced direct plant defences (Karban and Baldwin 1997). Foliar herbivory can also results in reduced attraction of bumblebee pollinators by the damaged plants, even though it does not result in changes in flower size and number (Kessler and Halitschke 2009). The induction of plant defences may go at the expense of other plant traits: resources may be reallocated from growth and development to defence, resulting in changes in plant phenology (Herms and Mattson 1992). Thus changes in plant performance may partly be caused by trade-offs between defence and other life-history traits.

Herbivory also induces the systemic production of leaf volatiles. These so-called herbivore-induced plant volatiles are often attractive to predators, which use these cues to locate their herbivorous prey (Turlings et al. 1990; Dicke et al. 1990; Sabelis et al. 2007). Moreover, they can affect the host plant choice by other herbivores (Pallini et al. 1997; Bernasconi et al. 1998; Shiojiri et al. 2002).

Not only herbivores may cause changes in plant performance, but omnivores may also do so. Several recent studies show that omnivores that cause limited or no damage to plants still induce plant defences (De Puysseleyr et al. 2011; Pappas et al. 2015; Pérez-Hedo et al. 2015a,b; Bouagga et al. 2018; Zhang et al. 2018 [= Chapter 2]; Chapters 3 and 4). Hence, like herbivory, plant feeding by omnivores may also cause changes in plant phenology, which is what we tested here. We previously showed that the omnivorous predator *Macrolophus pygmaeus* induced defences in sweet pepper plants, resulting in negative effects on performance of two herbivore species, i.e., the spider mite *Tetranychus urticae* and the thrips *Frankliniella occidentalis*. A third species, the aphid *Myzus persicae*, was unaffected (Zhang et al. 2018 [= Chapter 2]). Here we investigated the effects of this omnivorous predator on plant performance by evaluating plant development and reproduction. We subsequently assessed the effects these plant changes on survival and reproduction of the omnivore.

Materials and methods

Plant material

Sweet pepper plants (*Capsicum annuum* L. Spider F1; Enza Zaden Beheer, Enkhuizen, The Netherlands) were grown from seeds in pots (14 cm Ø) with soil in a climate room dedicated to growing clean plants (25 ± 1°C, 60-70% RH, 16:8 L:D). Water was supplied twice a week. Four-week-old plants with 6-8 true leaves (about 20 cm high) were used for experiments.

Cultures

A culture of *M. pygmaeus* was established with fifth-instar nymphs obtained from a commercial company (Koppert Biological Systems, Berkel en Rodenrijs, The Netherlands). They were reared in plastic containers (45 cm high, 35 cm Ø) in a climate room (conditions as above) with *Ephestia kuehniella* eggs as food and green bean pods as both food supply and oviposition substrate. New *E. kuehniella* eggs and beans were added twice a week. Old beans with *M. pygmaeus* eggs were transferred to new containers, and kept until the eggs hatched, whereupon *E. kuehniella* eggs and bean pods were supplied twice a week. Old pods from which nymphs no longer hatched were removed from the containers. Adults of 4-8 days old were used for experiments.

Experiment

Four-week-old plants with 6-8 true leaves were transferred into insect-proof cages (BugDorm-44590DHF, 93.0 × 47.5 × 47.5 cm, mesh size: 160 µm) that were equally distributed on three benches in a compartment in the greenhouse (25 ± 1°C, 60-70% RH, 16:8 L:D). Plants were watered twice per week and fertilized once per week. In half of the cages, five adult females and five adult males of *M. pygmaeus* were released, and plants in the other half of the cages were clean, serving as control plants. To minimize the effect of variation in abiotic factors among locations, plants with different treatments were alternated, and the sequence of treatments of the plants was alternated on different benches. Thereafter, numbers of females and nymphs of *M. pygmaeus* were assessed twice per week. No extra food was supplied for *M. pygmaeus* during the experiments. To keep densities of the omnivores similar throughout the experiment, the cages that contained fewer than five females of *M. pygmaeus* received new females and the same number of males twice per week, adding up to five females in each cage. This also resulted in assessment of survival of the omnivores. Leaves bigger than 8 cm were counted twice per week. After the first open flower appeared on one of the plants, the open flowers and fruits on the plants were counted on a daily basis, and the dates on which the first flower and fruit appeared on each plant were also recorded. Because *M. pygmaeus* feeds on pollen and nectar (Vandekerkhove and De Clercq 2010; Messelink et al. 2011), we compared the survival of females and the numbers of nymphs, resulting from reproduction of the omnivores, on the plants before and during flowering. Subsequently, we assessed the effects of the numbers of flowers on adult survival and on the number of nymphs, omitting the data before flowering. The survival of females and the numbers of nymphs on plants with and without flowers were also assessed.

Sixteen to 17 days after the onset of flowering, all plants were harvested, and leaves and stems and fruits of each plant were put in separate paper bags. The fresh

weight and the length and diameter of each fruit were measured, and the numbers of seeds in fruits heavier than 3 mg were assessed. Thereafter, all plant material was dried separately in an oven (Ehret KLT/S 2, Emmendingen, Germany) (80 ± 1°C) for about 2 weeks. Subsequently, dry weight of leaves and stems and fruits were recorded. The experiments were conducted in two blocks in time (Block A: October-November, 2016; Block B: March 2017), with nine plants per treatment per block.

Data analysis

The numbers of leaves, open flowers and fruits (all square-root transformed) on plants exposed to *M. pygmaeus* and clean plants were each compared using linear mixed-effect models (LME) with treatment, time and their interaction as fixed factors, and block and individual plant as random factors. The distribution of the residuals was checked for normality. Non-significant interactions and factors were removed until a minimal adequate model was reached (Crawley 2007). Contrasts were assessed with the Tukey method (function glht of the package lsmeans in R, Lenth 2016). We furthermore compared the time of the first flower appearing between treatments with a generalized linear model (GLM) with treatment and block as factors and a quasi-Poisson error distribution. Because flowers were not marked and followed through time individually, we estimated the time to fruit set as the difference between the appearance of the first flower and the first fruit per plant. These data were compared between treatments with a GLM with a Poisson error distribution and block and treatment as factors.

The total dry weight of the stem and leaves (untransformed) and the dry weight of the fruits [log(x+0.1)-transformed] per plant were each compared with LME with treatment as a fixed factor, and block and each individual plant as random factors as explained above.

The numbers of seeds per fruit may have been affected by the presence of *M. pygmaeus* and the volume of the fruit; therefore, we calculated the volume of all fruits heavier than 3 mg using half the volume of an ellipsoid as an approximation of the shape of a sweet pepper fruit. The numbers of seeds per fruit (square-root transformed) were compared using an LME as described above, with treatment and fruit volume and their interaction as fixed factors, and block and each individual plant as random factors.

The proportions of female omnivores surviving and the numbers of nymphs [log(x+1) transformed] on plants before and during flowering were compared using an LME as described above, with the presence of flowers as a fixed factor, and block and plant as random factors. The analysis of the numbers of nymphs as a function of the numbers of flowers was done with a similar LME, with block as a random factor. Survival of adult females as a function of the number of flowers was done with a
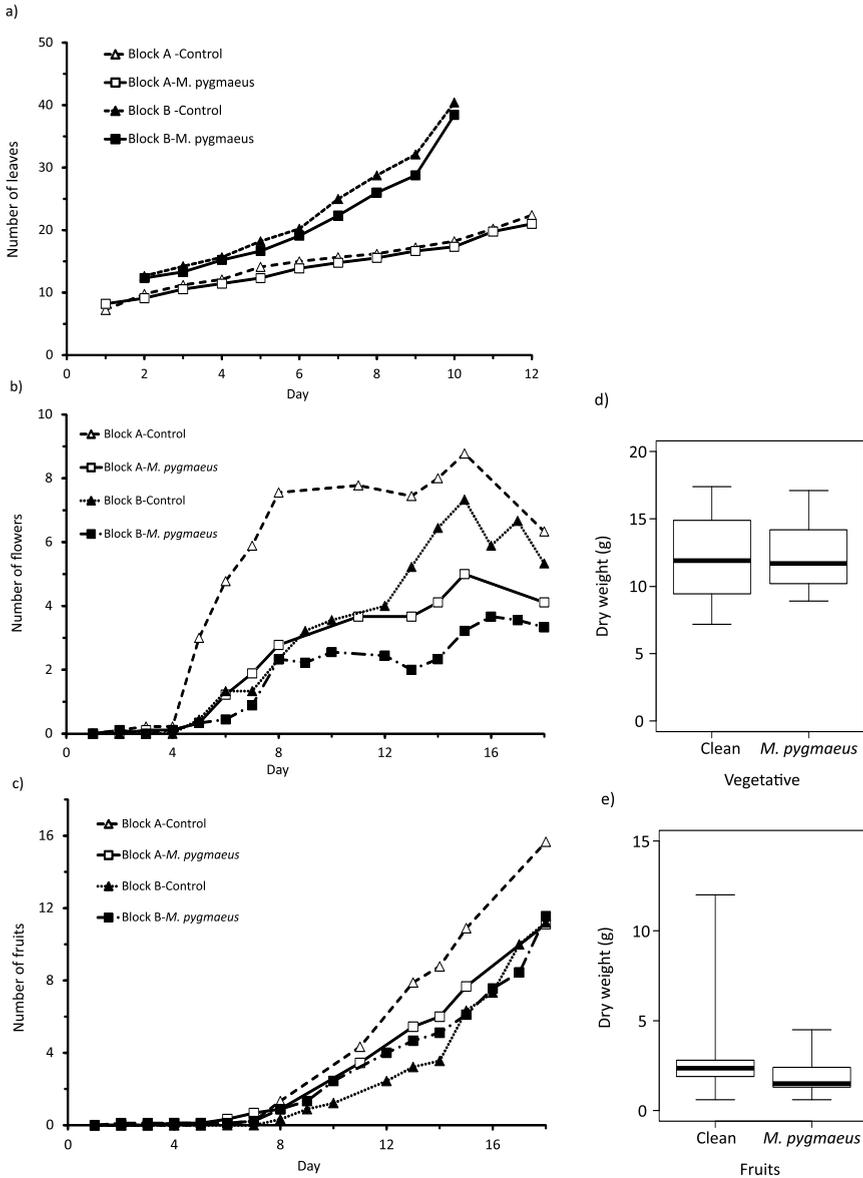
FIGURE 5.1 The average numbers of leaves (a), flowers (b) and fruits (c) on sweet pepper plants exposed to *Macrolophus pygmaeus* and clean plants over time in two experimental blocks performed in different seasons. Triangles indicate clean plants (Block A: open triangles; Block B: closed triangles); Squares indicate plants exposed to *M. pygmaeus* (Block A: open squares; Block B: closed squares). Standard errors are not shown for reasons of clarity. The median dry weights of leaves plus stems (d) and fruits (e) on plants exposed to *M. pygmaeus* and clean plants. Vertical thick lines show medians, boxes show 25th and 75th percentiles and whiskers give minima and maxima

generalized mixed effects model (GLMER) with a binomial error distribution (logit link) and with block and plant as random factors. All statistical analyses were performed with R (R Core Development Team 2017).

Results

Plants exposed to *M. pygmaeus* had significantly lower numbers of leaves than clean plants (Figure 5.1a, LME: $\chi^2 = 5.75$, d.f. = 1, $P = 0.017$), and the numbers of leaves from both groups of plants increased with time (LME: $\chi^2 = 513.2$, d.f. = 1, $P < 0.0001$). The numbers of leaves differed between the two blocks (Figure 5.1a), which was probably caused by the two blocks having been conducted at different periods. There was no significant difference between treatments in the timing of the first flower (clean plants: average = 5.28 ± 0.61 days, *M. pygmaeus*-treated plants: 6.56 ± 0.79 days, GLM, $F_{1,34} = 1.89$, $P = 0.18$). The numbers of open flowers on plants with and without *M. pygmaeus* increased differently with time (Figure 5.1b, LME: interaction of treatment and time, $\chi^2 = 7.4$, d.f. = 1, $P = 0.0064$). Plants exposed to *M. pygmaeus* had lower numbers of flowers than clean plants (Figure 5.1b, contrasts after LME). The numbers of fruits of both groups of plants increased differently with time (Figure 5.1c, LME: $\chi^2 = 4.5$, d.f. = 1, $P < 0.034$), but overall did not differ significantly (Figure 5.1c, contrasts after LME). The difference in time between appearance of the first flower and the first fruit was approximately half on exposed plants than on
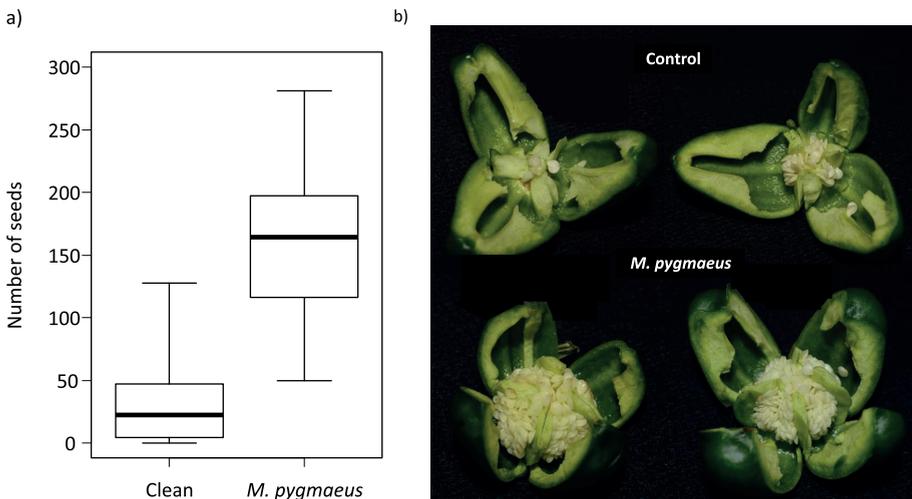

Figure 5.2 The median numbers of seeds in each fruit from sweet pepper plants exposed to *Macrolophus pygmaeus* and clean plants (a) and a picture showing numbers of seeds in two fruits from control plants (top) and *M. pygmaeus*-exposed plants (bottom) (b). Vertical thick lines show medians, boxes show 25th and 75th percentiles and whiskers show minima and maxima

clean plants (*M. pygmaeus*-treated plants: 2.5 day ± 0.26 days; clean plants: 4.8 day ± 0.29 days, GLM: χ^2 = 13.8, d.f. = 1, P < 0.001).

Plants with and without *M. pygmaeus* had similar biomass of leaves plus stems (FIGURE 5.1d, LME: χ^2 = 0.07, d.f. = 1, P = 0.80). However, there was a non-significant trend of the total dry weight of fruits from plants with *M. pygmaeus* being lower than that of clean plants (FIGURE 5.1e, LME: χ^2 = 3.2, d.f. = 1, P = 0.072).

Interestingly, plants exposed to *M. pygmaeus* produced five times higher numbers of seeds per fruit than clean plants did (FIGURE 5.2ab, LME: χ^2 = 41.6, d.f. = 1, P < 0.0001), which was not affected by the volume of the fruits (LME: χ^2 = 2.11, d.f. = 1, P = 0.15).

The survival rate of female *M. pygmaeus* was higher when plants were flowering than before flowering (FIGURE 5.3a, LME: χ^2 = 51.0, d.f. = 1, P < 0.0001), and there were also more nymphs on plants during flowering than before flowering (FIGURE 5.3b, LME: χ^2 = 24.6, d.f. = 1, P < 0.0001). Adult survival increased with the numbers of flowers (FIGURE 5.4a, GLMER, χ^2 = 11.75, d.f. = 1, P = 0.0006), as did the number of nymphs (FIGURE 5.4b, LME, χ^2 = 9.15, d.f. = 1, P = 0.0025).

Discussion

We show that exposure of sweet pepper plants to the omnivorous predator *M. pygmaeus* affected plant performance. Plants exposed to the omnivores had significantly lower numbers of leaves and open flowers than clean plants, suggesting that the
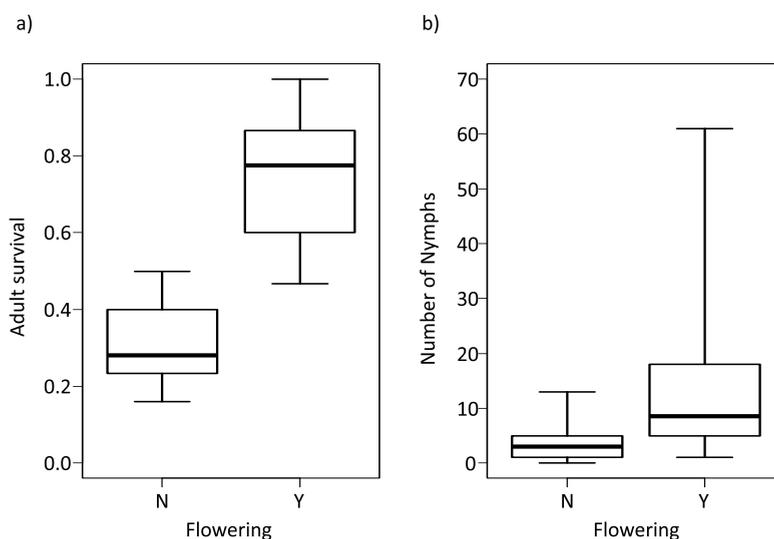

FIGURE 5.3 The median proportion of surviving females (a) and the median numbers of nymphs (b) of *Macrolophus pygmaeus* on plants with (Y) and without (N) flowers. Vertical thick lines show medians, boxes show 25th and 75th percentiles and whiskers show minima and maxima

presence of *M. pygmaeus* had a negative effect on these plants. Similar numbers of fruits and similar dry weights of leaves plus stems and fruits were found on plants exposed to the omnivore and clean plants, showing no negative effects on plant performance. Moreover, omnivore exposure significantly shortened the time from the first flower to the first fruit, and five times higher numbers of seeds per fruit were
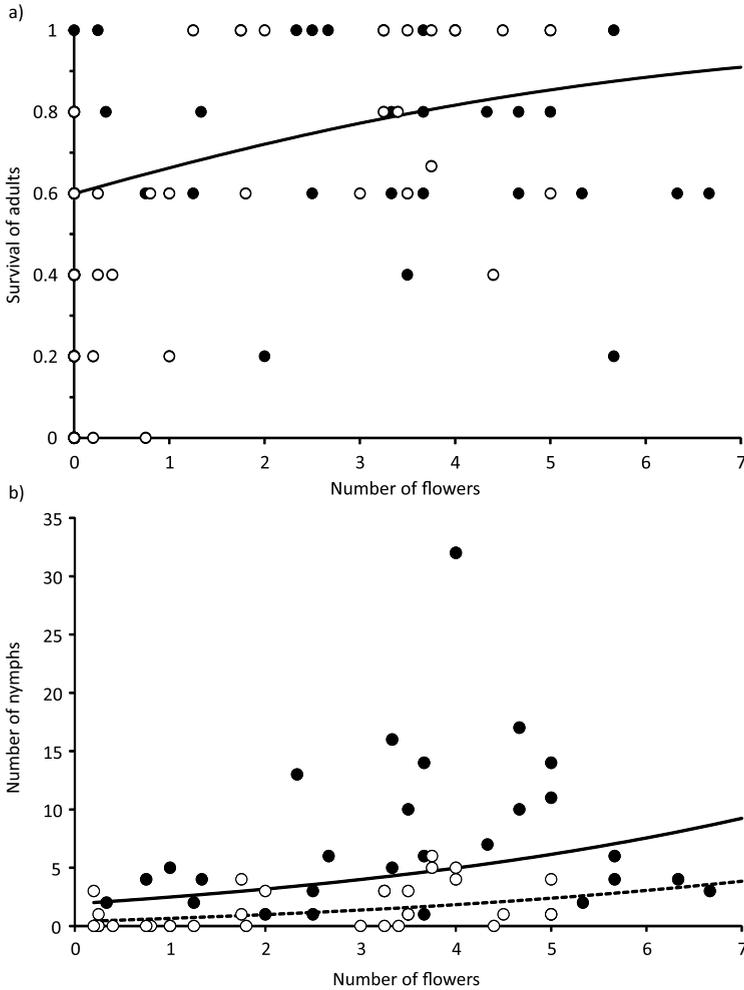

FIGURE 5.4 The effect of the number of flowers on the survival of *Macrolophus pygmaeus*. a) The proportion of females surviving in two blocks (Block A: closed circles; block B: open circles). The solid line is the fitted curve of a generalized linear mixed effects model on data of both blocks together (block did not have a significant effect). b) The numbers of nymphs in two blocks. Lines indicate the relation between the number of nymphs and the number of flowers in two blocks (Block A: solid line; block B: dashed line)

found on plants with omnivores than on clean plants, suggesting that the presence of the omnivore is not costly but beneficial for plant fitness. For logistic reasons, we did not measure plant performance throughout individual plant lifetimes. Possibly, effects of *M. pygmaeus* on plant growth and flowering can be partly compensated later in the plant's life.

Before the plants started flowering, the omnivores could only use leaves and stems as food source. After the plants started flowering, they could also feed on pollen and nectar, which resulted in increased survival and development of the omnivore, as was found previously (Perdikis and Lykouressis 2000). This shows that the omnivores benefit from the resources offered by the flowers. Indeed, *M. pygmaeus* is often found in the flowers of sweet pepper plants (Messelink and Janssen 2014). The results presented here show that the presence of this omnivore resulted in earlier fruit development and in higher numbers of seeds per fruit, suggesting that *M. pygmaeus* may also act as a pollinator. Sweet pepper is self-pollinating, but movement of the flowers is needed for pollination. Under greenhouse conditions, wind causes sufficient movement, thus growers do not need to release pollinators. In the cages used in our experiment, there was no wind, so pollination may have occurred less in cages without the omnivore.

The other changes in plant phenology, i.e., lower numbers of flowers and leaves, may have been a consequence of the exposed plants allocating more resources to fruits than to flowers and leaves. In our experiments, plants may have invested in fruits rather than flowers because the presence of *M. pygmaeus* probably increased pollination. However, the phenological changes could also have been a consequence of the plant investing more in induced plant defences. Earlier, we showed that plant feeding by the omnivore resulted in the induction direct plant defences, which affected the performance of the spider mite *Tetranychus urticae* and the thrips *Frankliniella occidentalis*, but not the aphid *Myzus persicae* (Zhang et al. 2018 [= CHAPTER 2]). The induction of such plant defences can result in the allocation of fewer resources to vegetative growth and flower production. Induced plant defences are often assumed to be costly because of this reallocation (Zangerl et al. 1997; Agrawal 2000), but there is mixed evidence for such costs (Karban 1993; Gianoli and Niemeyer 1997; Thaler 1999; Strauss et al. 2002). The results presented here suggest that plant performance is not negatively affected by the presence of *M. pygmaeus* on the plant or by the induction of plant defences by the omnivore. Clearly, the ultimate proof for costs of induced plant defences and other changes in the plant caused by the omnivore, should involve ecological costs because of changes in interactions within the entire food web associated with the plant (Sabelis et al. 2007).

One may wonder why plant defences are induced by plant feeding by *M. pygmaeus*? This omnivore does not cause significant damage to plants, and can effec-

tively protect plants against herbivores, making induced plant defences largely redundant. Perhaps the omnivore mainly visits plant in nature that have already been attacked by herbivores, and further induction by the omnivore will then have little effect on plant defences and plant fitness. Furthermore, it is known that omnivores feed more on prey and less on the plant when plant quality is low (Agrawal et al. 1999; Janssen et al. 2003). Possibly, the induction of plant defences by *M. pygmaeus* lowers plant quality, resulting in a preference for pollen, nectar and herbivores in the omnivores, thus promoting fruit development and seed production as well as reducing plant damage.

One remaining question is how *M. pygmaeus* interacts with other pollinators and how this affects fruit and seed production (Lehtilä and Strauss 1997; Strauss et al. 2002; Bruinsma et al. 2008, 2014). As explained above, sweet pepper plants are self-pollinating, and are not dependent on pollinators in greenhouses or in the field. However, on other plant species, the omnivore could directly interact with pollinators by attacking them in the flowers, and indirectly by inducing plant defences. It is known that herbivory can affect pollinator behaviour (Kessler and Halitschke 2009), and the induction of plant defences by *M. pygmaeus* may have similar effects. Possibly, plant feeding by the omnivore can affect pollen and nectar characteristics, which may influence the behaviour of pollinators. This clearly needs further investigation.

The survival of *M. pygmaeus* on flowering plants was higher than plants without flowers. Furthermore, there was a positive relation between the survival and reproduction of the omnivore and the number of open flowers. Because plants exposed to the omnivore produced fewer flowers, this suggests that the changes in flowering as a result of this exposure do not benefit the omnivore. This may further cause the omnivores to feed on herbivores instead of on pollen and nectar. Thus, it appears that the changes in plants as a result of exposure to the omnivore benefit the plant and not the omnivore.

Macrolophus pygmaeus is commercially used for pest control in greenhouses. The large advantage of plant feeding by this omnivore for biological pest control is that populations can be established in a crop before pest outbreaks. Here we show that such plant feeding has no effect on fruit biomass while it increases seed production.

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